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MULTIPLICATION BY FISSION IN HOLOTHURIANS[1]

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THERE is to be found in various text-books the statement that certain pedate holothurians are capable of spontaneous transverse division, each part so formed producing a new individual (Lang, 1894, p. 1095; Morgan, 1901, p. 144). This opinion seems to be based, so far as I can learn, upon the observations of Dalyell (1851, p. 74; Pl. XIV), although Morgan says that "more recent observers have confirmed this discovery." Chadwick (1891), also, found small individuals of *Cucumaria planci* to undergo self-division, and in one instance the posterior portion so formed also divided. These are records of division in holothurians which were being kept in small aquaria, and there has been no evidence, so far as I am aware, going to show that self-division of adult pedate holothurians is a method of propagation among these animals in their normal surroundings. Hence the possibility of non-sexual reproduction in this way is usually stated with reserve (cf. Lang, 1894).

In other classes of echinoderms (aside from echinoids) the expedient of reproduction by fission is of course not unusual; but in ophiuroids and in such starfishes as *Linckia* (Clark, 1913) and *Coscinasterias* (Crozier, 1914),[2] we are dealing with the division or fragmentation of a many-armed creature relatively deficient in morphological centralization; whereas in *Cucumaria* and in *Holothuria* the body is compactly built, the animal much more of a unified individual. Consequently the self-division of these holothurians is not without interest, especially since in these cases the plane of separation is anatomically perpendicular to that employed among the astroradiates, and it is the purpose of this paper to present evidence which proves that adult specimens of at least one species, *Holothuria surinamensis* Ludw., do as a matter of fact divide transversely into two parts under conditions which must be regarded as normal. Since these divisions are not infrequent in large numbers of specimens, if not in a single life-history, we must conclude that fission represents a regular means of mutliplication in this species.

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[2] I have been able to secure further evidence regarding the fragmentation of *Coscinasterias* (*Asterias*) *tenuispina* (Lam.), which proves conclusively that the rules previously deduced (Crozier, 1915*a*) regarding this process are indeed valid. This evidence will be published in connection with a description of experiments on the direction of progression in *Coscinasterias*. The presence of great variation in ray-length, as well as of a variable number of madreporites, gives an opportunity to test out in this species the validity of certain ideas concerning "physiological polarization" in asteroids.

A few years ago I found (Crozier, 1915*b*) that about 10 per cent. of the examples of *H. surinamensis* which were studied showed a condition of either the oral or of the cloacal end which—on the basis of observed regenerations following experimental cutting—I interpreted as representing regeneration, possibly as a consequence of spontaneous self-division. Similar conditions have been noted by others for some other species of holothurians, *e. g.*, by Benham (1912, p. 136) for *Actinopyga* (*Mülleria*) *parvula* (Selenka), but they have usually been referred to regeneration after injury by such bottom feeding fishes as small sharks. Dr. H. L. Clark informs me that he has found a corresponding state of affairs in some Australasian holothurians, at least in regard to the occurrence in nature of specimens showing posterior regeneration.

I subsequently obtained young individuals of *H. captiva* Ludw., about 6 mm. in length, which were observed to divide spontaneously in the laboratory (Crozier, 1914, p. 18), precisely according to the procedure figured by Dalyell (1851) and by Chadwick (1891). Only a single adult *H. captiva* has been discovered, however, in which there was evidence of normal regeneration; this individual, which was 40 mm. long, was obtained among a group of 47 taken from under a large rock in April, 1916.[3] The anterior end for a distance of 7 mm. from the tip was light greenish yellow, with ten very feebly developed tentacles; there was a sharp line of demarcation between the light yellow surface and the dark olive green of the rest of the body. If *H. captiva* undergoes division normally, it can only occur in very young stages.

With *H. surinamensis*, however, the case is quite different. In Table I there are summarized results of the examination of several series of these animals collected at different times for this particular purpose. It will be noted that in these collections from 2.5 to 16.9 per cent. (on the average about 11 per cent.) of the individuals show a condition of either the oral or of the cloacal end which is interpreted as representing regeneration. This seems to be about the proportion of such instances which is to be met with in general collecting, although numerical records have been kept only in the cases cited. The specimens represented in the tabulation were obtained from one locality, Fairyland Creek, where they notably abound; but the species has been collected at many other stations, where also the regenerating individuals are to be found in approximately the same proportion. The

TABLE I

THE RELATIVE NUMBER OF CASES IN WHICH *Holothuria surinamensis* WAS FOUND TO BE REGENERATING IN NATURE

Date	No. examined	Regenerating			
		Oral	Cloacal	Total	%
June, July, 1913	200	7	13	20	10.0
July 30, 1916	39	0	1	1	2.5
Aug. 26, 1916	84	6	5	11	13.1
Jan. 25, 1917	70	6	3	9	12.8
Jan. 31, 1917	53	4	5	9	16.9
Total	446	23	27	50	11.2

Ratio of regenerating oral to cloacal ends = 1 : 1.17.

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[3] It is known that some holothurians tend to congregate together in considerable numbers at their time of breeding. Graber considered this to indicate the presence of a chemical sense (Delage et Hérouard, 1903).

season of the year seems not to influence the occurrence of regenerating specimens.

The criterion of regeneration in these cases consists in the presence of an anterior or posterior terminal part of the body characteristically different in appearance from the normal buccal or cloacal end, the surface being clearly marked off from that of the rest of the body. In typical examples these regenerated ends of the animal are more sharply pointed than is usual; they bear feebly developed tentacles (at the anterior end), tube feet, and dorsal papillæ, which are less reactive than those on animals judged to be not regenerated; and these appendages are very lightly pigmented (Fig. 1). These characteristics

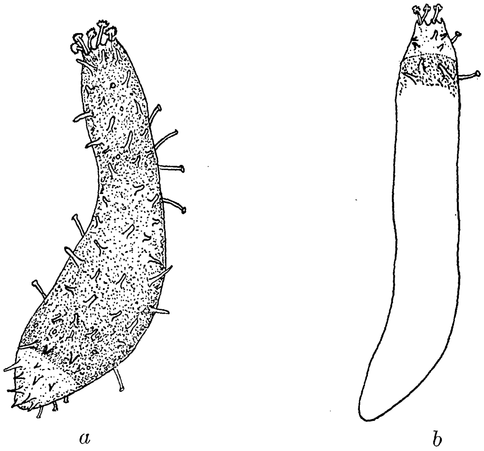

FIG. 1. Regeneration found occurring naturally. Semidiagrammatic sketches, showing differences in pigmentation of *a*, cloacal end, *b*, oral end. Natural size.

undoubtedly become less prominent with time, the coloration tending, however, to remain pale on the ventral surface (trivium). The first pigment to appear is the green fluorescent one (cf. Crozier, 1914, p. 9 and 1915*b*); the dark brown substance develops more slowly, just as in the growth of the post larval holothurians of this and related species. The spicules of the podia and skin seem fewer than in corresponding non-regenerating parts, but are of the usual sizes and shapes. The tentacles on regenerating buccal ends are always fewer (9–15) than on the normal individual (20).

That the oral and cloacal terminations just described do in reality represent regeneration, has been verified by observation of the course of regeneration in the laboratory after experimentally cutting the holothurians in various ways (cf. Crozier, 1915*b*). Certain specimens also have been tabulated as "regenerating" when their appearance (Fig. 2, *c*), backed up by dissection, suggested that they had just completed division and had not yet begun to regenerate. These specimens lacked either a cloaca, or the stone ring and buccal structures, depending, obviously, on their former relation to the complete individual from which they were derived.

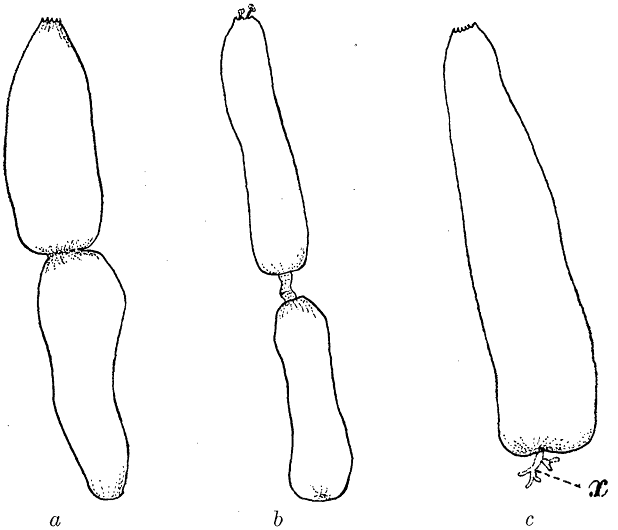

FIG. 2. Outlines of individuals dividing or recently divided. In *a* and *b* the division is shown in progress, × ½ ; in *b* the exposed portion of the undivided intestine is visible; in *c* is given the outline of a recently separated oral half, natural size. At *x* is seen a protruding bit of the portion of the respiratory trees retained within this half animal. The characteristic puckering of the surface at the division area is also indicated.

The evidence that the regeneration found occurring under natural conditions results from the self-division of adult holothurians, involves two considerations. The first concerns (*a*) the relative size of the regenerating animals, and (*b*) the relative frequency of anterior and posterior ends noted as regenerating. The second has to do with direct observations of self-division.

One hundred *H. surinamensis* collected in Fairyland Creek ranged in length from 6 to 18 cm., with the mode at 14 cm. The regenerating specimens ranged in length from 4 to 9 cm., with the mode at 7 cm. While no numerically exact argument can be based on these figures, since the length of any one holothurian is variable, the fact does stand out that the regenerating animals are about one half the length of the non-regenerating ones. There is also the significant fact that not a single instance has been found in which both a (supposedly) new oral and new cloacal end were present. If self-division has occurred, then we should expect to find new oral and new cloacal extremities in equal frequency; among the rather small number of cases available, we find their ratio to be as 1:1.17, an agreement sufficiently close to favor belief in self-division.

The evidence concerning the second point is even more conclusive. I have seen, in all, nine cases in which a holothurian (*H. surinamensis*), in the laboratory, divided itself into two parts. The animals concerned seemed healthy, and bore no visible signs of having been in any way injured. In no case did the halves so formed redivide, although in two cases the resulting portions lived in the laboratory for a month (Aug. 3 to Sept. 5, 1916), during which time, even in the absence of food, missing structures were regenerated.

In one case the process of division occupied five days; in another, twenty-four hours. Probably it is executed more rapidly in the field. The details of the division were not notably different from those described by Chadwick (1891) for *Cucumaria*, except perhaps in one particular. The intestine is not drawn out between the separated halves, as found in *Cucumaria* and as I have observed in the young of *H. captiva*. Division begins midway of the length of the body with a deep insinking of the "dorsal" bivium. A powerful circular constriction, accompanied by some slight local disintegration of the integument, completes the separation (Fig. 2). During the progress of division the animal is quiescent, although it may be adhering firmly by its tube feet to the vertical wall of the aquarium. When the constriction and separation of the skin- and muscle-layers is completed, a short length of the intestine usually remains for a time connecting the two pieces; it may rupture close to one of them, or may disintegrate completely. The point to be noted is, that the resultants of the division do not move apart, but remain quiescent.

Lastly, after considerable searching, I found in the field one case in which division had evidently just been completed. The halves were still joined by an exposed portion of the gut.

On the basis of all this evidence there is certainly reason to believe that *Holothuria surinamensis*, in the adult state, normally multiplies its numbers by a process of binary fission. The resulting organisms readily complete their missing parts, but probably do not undergo a second division until after the lapse of a considerable interval, if they do at all.

It would be of some interest to determine the nature of the sexual products in the animals which thus result from division.

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BERMUDA

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